U.S. DEPARTMENT OF COMMERCE
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PB-287 000

Mortality Rates from Size Distribution The Application of a Conservation Law

(U.S.) Corvallis Environmental Research Lab, OR

Prepared for

National Research Council, Washington, DC

1 Oct 76

TECHNICAL REPORT DATA
(Please read Instructions on the reverse before completing)

1. REPORT NO. EPA-600/J-77-131	2. JOURNAL ARTICLE
	PB 287000
4. TITLE AND SUBTITLE MORTALITY RATES FROM SIZE DISTRIBUTION: THE APPLICATION OF A CONSERVATION LAW	5. REPORT DATE
	6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S) John VanSickle	8. PERFORMING ORGANIZATION REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS Ecosystems Modeling & Analysis Branch U.S. Environmental Protection Agency Corvallis Environmental Research Laboratory 200 S.W. 35th St. -- Corvallis, OR 97330	10. PROGRAM ELEMENT NO. 1BA608 11. CONTRACT/GRANT NO.
12. SPONSORING AGENCY NAME AND ADDRESS National Research Council 2101 Constitution Ave., N.W. Washington, D.C. 20418	13. TYPE OF REPORT AND PERIOD COVERED 14. SPONSORING AGENCY CODE EPA/ORD

15. SUPPLEMENTARY NOTES
Published in Oecologia Vol. 27,pp311-318

16. ABSTRACT

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17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group
Population model; Size distribution; Mortality; Age distribution; Mortality estimates		05/K

18. DISTRIBUTION STATEMENT Release Unlimited	19. SECURITY CLASS *(This Report)* unclassified	21. NO. OF PAGES 9
	20. SECURITY CLASS *(This page)* unclassified	22. PRICE A02-A01

EPA Form 2220-1 (9-73)

REPRODUCED BY
NATIONAL TECHNICAL
INFORMATION SERVICE
U.S. DEPARTMENT OF COMMERCE
SPRINGFIELD, VA. 22161

Oecologia (Berl.) 27, 311 – 318 (1977)

Oecologia
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EPA-600/J-77-131
JOURNAL ARTICLE

Mortality Rates from Size Distributions

The Application of a Conservation Law*

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Summary. A population model explicitly describing the dynamics of an arbitrary population size distribution is presented. One consequence of the model is an equation for the exact shape of the size distribution of a stationary or steady-state population. The shape is expressed as a function of size-specific mortality and growth rates. From the equation, various mortality estimation formulas can be derived, two of which are discussed in detail. One of the methods permits estimation of size-specific mortality rates without the assumption of a theoretical growth model.

Introduction

For most biological populations, size-frequency distributions are much easier to obtain than age distributions. As a result, repeated attempts have been made to analyze size data, usually for the purpose of estimating mortality rates. Ebert (1973) gives a brief summary of these methods, all of which employ a common strategy – growth data and dynamic age distribution models are combined to give descriptions of the population's size distribution.

Because there is no simple relationship between age and size distributions, the techniques require fairly restrictive assumptions about growth and mortality rates. For example, the models of Smith (1972) and Ebert (1973) assume that growth is described by the Brody-Bertalanffy function (Bertalanffy, 1957) and that mortality is constant over all body sizes.

An alternative strategy is to deal directly with the dynamics of the size distribution. This approach makes use of size-specific, rather than age-specific, mortality and growth rates as vital parameters in a conservation equation for population number density. When the model is applied to populations which are assumed to have fixed age and size distributions, it yields a formula for the instantaneous mortality rate as a function of individual growth rate and the shape of the size distribution. As a result, mortalities can be estimated directly from observed size-

* Supported by a National Research Council Research Associateship

frequency curves and growth data, without explicitly determining the population's age distribution.

The Model

Suppose that a population's size distribution is specified by a number density function, $N(z, t)$, with the meaning that

$$\int_{z_1}^{z_2} N(\bar{z}, t)\, d\bar{z}$$

is the total number of individuals in the size interval (z_1, z_2) at time t.

Also assume that $g(z) = dz/dt$ is the size-specific, absolute growth rate of individuals. The function $g(z)$ must be positive. For any particular population, $g(z)$ could be determined directly from size-at-age data, or it might be specified by a theoretical curve such as the Brody-Bertalanffy function. In the latter case, for example, if z_∞ is the asymptotic body length and k the rate parameter, then

$$g(z) = k(z_\infty - z). \tag{1}$$

In addition, assume that instantaneous mortality rate is a size-specific function, $\mu(z)$.

Given these assumptions, the dynamics of the number density are described by the following conservation equation for the "flow" of organisms through the size distribution:

$$\frac{\partial N(z,t)}{\partial t} + \frac{\partial}{\partial z}[g(z)\, N(z,t)] = -\mu(z)\, N(z,t). \tag{2}$$

Models of the same form as (2) were first proposed by Von Foerster (1959) for cell dynamics and have since been applied to a variety of populations, including shrimp (Billups et al. 1971), *Daphnia* (Sinko and Streifer, 1969), and insects (Lee et al., 1976).

Sinko and Streifer (1967), among others, have derived Equation (2), and the derivation will not be repeated here because of its length. However, the conservation equation may be roughly interpreted as follows: the first term, $\frac{\partial N(z,t)}{\partial t}$, represents the net rate of change in numbers of individuals in a thin size interval, $(z, z+dz)$. This rate is the sum of two terms. The first term, $\left(-\frac{\partial}{\partial z}[g(z)\, N(z,t)]\right)$, is the net loss rate of individuals due to growth through the interval $(z, z+dz)$. The second term, $[-\mu(z)\, N(z,t)]$, is the loss rate from $(z, z+dz)$ due to mortality.

To provide a complete description of a self-sustaining population, a size distribution must be specified at time $t=0$, and Equation (2) must be coupled to a model for reproduction. The reproduction model, which may in turn depend on the size distribution, $N(z,t)$, serves as a boundary condition for Equation (2). Several such models are discussed by Oster and Takahashi (1974) and by Van Sickle (1975, 1977). For the purposes of this paper, it is sufficient to define an arbitrary recruitment function, $R(t)$. $R(t)$ is the rate of appearance of new individuals

of size z_R, where z_R the size of the smallest organism observed in a particular population.

Once an initial distribution and a reproduction function are specified, Equation (2) can be solved analytically to describe the dynamics of a population size distribution (Van Sickle, 1975, 1976).

Conservation models for the number densities of size or age distributions can be extended to more realistic and general equations which retain the same form as the model (2). Growth, mortality, and fertility rates may become time-varying, and terms might be added to account for immigration. Equation (2) is also expanded if individuals are categorized by more than one measure of body size, or by age and size. Reviews of the theory and applications of population conservation equations can be found in Streifer (1974) or Oster and Takahashi (1974).

Stationary Distributions

The model (2) takes on a particularly simple form when $N(z, t)$ is the size distribution of a stationary population. In this case, the size and age distributions are fixed, and $R(t)$ is constant and equal to the population death rate. Equation (2) becomes a model of such a population when $\frac{\partial N(z, t)}{\partial t}$ is set identically equal to zero. Then the stationary size distribution, $N_s(z)$, satisfies

$$\frac{d}{dz}[g(z)\,N_s(z)] = -\mu(z)\,N_s(z). \tag{3}$$

Equation (3) can also be written as

$$\frac{d}{dz}[\ln N_s(z)] = -\left[\frac{\mu(z)+g'(z)}{g(z)}\right], \tag{4}$$

where $g'(z) = \frac{dg(z)}{dz}$.

Equation (4) clearly shows how a stationary size distribution is shaped by growth and mortality. In another paper (Van Sickle, 1976), I discuss how Equation (4) gives a quantitative interpretation to the peculiar shapes appearing in size distributions whenever organisms "stack up" in size due to decreasing growth rates. The equation also suggests that, when a population is stationary, mortality can be estimated from observations of $N_s(z)$ and a knowledge of growth rate.

Few populations have a constant birth rate, and the concept of stationarity may be broadened to include seasonally-breeding species. A stationary population is also defined as one having age and size structures which are cyclic, with a period usually of a year (Seber, 1973). On an annual basis, births equal deaths, and size distributions observed at yearly intervals appear identical. This type of population has also been called "steady-state" by Beverton and Holt (1957). It can be shown that Equation (4) remains valid for steady-state populations if $N_s(z)$ is taken to represent an annual "average" size distribution, rather than a distribution at one point in time (Van Sickle, 1975).

Mortality Estimation

Equation (4) serves as a basis for estimating mortality rates in steady-state populations whenever growth and size-frequency data are available. If (4) is solved for $\mu(z)$, it becomes

$$\mu(z) = -g(z)\frac{d}{dz}[\ln N_s(z)] - g'(z). \tag{5}$$

Various mortality estimation methods can be derived from (3), (4), or (5) to suit different configurations of the data. I will describe two quite different methods and present sample computations.

Method 1

Because of sketchy data or the desire for a rapid, rough estimate for $\mu(z)$, one could simply replace each of the functions in (5) with an estimate of its average value over all or part of the body size spectrum. Then (5) is written:

$$\hat{\mu} = -\hat{g}\,\hat{s} - \hat{g}'. \tag{6}$$

In (6), the $\hat{}$ signifies a mean value with respect to size, and $\hat{s}$ is the estimate of the slope of $[\ln N_s(z)]$ over the size range of interest.

In the simplest case, growth rate would be constant, so that $\hat{g}' = 0$. Then Equation (6) is identical to Baranov's method of mortality estimation, as discussed by Ricker (1958). Ricker points out that mortality rates computed from the equation $\hat{\mu} = -\hat{g}\,\hat{s}$ "... always tend to be too small, if absolute rate of increase in [size] is decreasing with age." This observation is confirmed by (6) in which the term $[-\hat{g}']$ acts as a positive correction factor for Baranov's formula, when growth rates decrease with size.

In most cases, $\hat{g}'$ is difficult to evaluate accurately, since it essentially is the second derivative of the original size-at-age data. However, if Brody-Bertalanffy growth can be assumed, then $g'(z) = -k$ [see Eq. (1)]. Now $\hat{k}$, an estimate of k, replaces $\hat{g}'$ in Equation (6). This gives the formula

$$\hat{\mu} = -\hat{g}\,\hat{s} + \hat{k}. \tag{7}$$

Both graphical and computer methods exist for fitting the Brody-Bertalanffy curve to growth data and obtaining $\hat{k}$. For a summary of these techniques, see Ricker (1975).

Example

Figure 1 is an annually-averaged size-frequency histogram for a population of Black abalone (*Haliotis cracherodii*) in California. A curve of growth rate versus shell length reported by Leighton and Boolootian (1963) indicates that growth rate is decreasing at a slow, steady rate over the range of 50 to 150 mm and can be modelled fairly well by a Brody-Bertalanffy function. For smaller individuals,

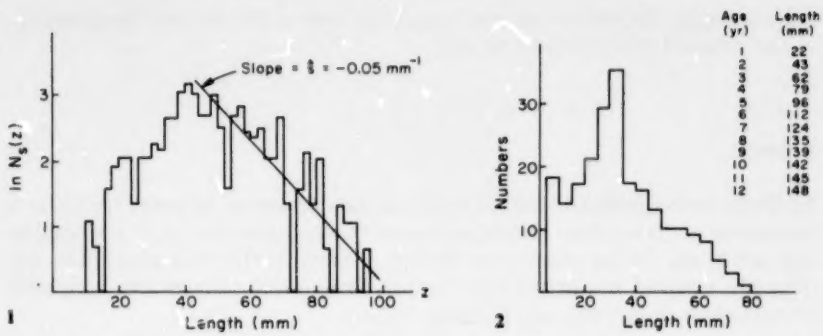

Fig. 1. Yearly average length distribution for *Haliotis cracherodii*. Data from Leighton and Boolootian (1963)

Fig. 2. Yearly average length distribution and growth of *Tivela stultorum*. Data from Coe and Fitch (1950), as cited by Smith (1972)

growth fluctuates widely. Leighton and Boolootian give a mean growth rate of $\hat{g} = 20$ mm/yr from 40 to 100 mm, and Smith (1972) estimated $\hat{k} = 0.13$ yr^{-1} using the graphical technique of Walford (Beverton and Holt, 1957; Ricker, 1975). As Figure 1 illustrates, $\hat{s} = -0.05$ mm^{-1}.

Substitution of these values into (7) results in $\hat{\mu} = 1.1$ yr^{-1}, which is equivalent to a 67% loss per year of individuals sized from 50 to 100 mm. This estimate is identical to the rate computed by Smith (1972).

Method 2

When comprehensive growth and size-frequency data are available, it is possible to estimate mortality on a size-specific basis. The full size spectrum is divided into size classes, indexed here by j, and it is assumed that mortality μ_j is the same for all individuals in size class j. The size classes may be of any width – the only requirement is that values for growth rate and number density be available at the boundaries of each class.

Let j stand for the size interval (z_j, z_{j+1}). Suppose the growth rates $g(z_j)$, $g(z_{j+1})$ and also the number densities, $N_s(z_j)$, $N_s(z_{j+1})$ are known. Further, suppose N_j^*, the total number or proportion of organisms in class j, is known. Then μ_j is computed from

$$\mu_j = \frac{1}{N_j^*}\left[g(z_j)\,N_s(z_j) - g(z_{j+1})\,N_s(z_{j+1})\right] \tag{8}$$

Equation (8) is obtained by integrating (3) from z_j to z_{j+1} and assuming that mortality is a constant, μ_j, over that interval.

This equation is by no means unique as a discrete approximation of the continuous distributions (3), (4), and (5). However, it does have the advantage of

not containing the derivatives and logarithms seen in the continuous equations, so that original data are easier to use.

Example

To illustrate the application of (8), I will use data presented by Smith (1972) for a population of Pismo clams (*Tivela stultorum*). Figure 2 gives the length distribution and size-at-age values, taken from Table 5 of Smith (1972). The population was originally sampled and analyzed by Coe and Fitch (1950). Growth data were used to define growth rate as a step function. That is,

$$\begin{aligned} g(z) = {} & 22 \text{ mm/yr}, && 0 \leqq z < 22 \text{ mm} \\ & 21 \text{ mm/yr}, && 22 \text{ mm} \leqq z < 43 \text{ mm} \\ & \vdots \\ & \text{etc.} \end{aligned}$$

Mortality rates were computed using (8) for each of the 5-mm size classes comprising Figure 2, and the rates μ_j are listed in Table 1. The size classes of Figure 2 often differ in numbers by only one or two clams, so the accuracy of individual size-specific rates in Table 1 is questionable. For this data set, the estimate should be restricted to an average rate taken over several size classes. However, the example does illustrate how size-specific mortalities are calculated when larger sample sizes are available.

Table 2 compares the averages from Method 2 with rates obtained by Smith and by Coe and Fitch (1950) for the same population. Smith combines the assumptions of stationarity, constant mortality, and Brody-Bertalanffy growth to obtain an equation analogous to (8) for the size distribution. Coe and Fitch's estimate, however, is obtained from tag-recapture sampling. Their values for mortality are probably the most accurate, since they are generated from an age-specific life table, while Method 2 and Smith's technique are time-specific (Seber, 1973).

As Table 2 shows, the average mortality from Method 2 for all size classes is quite different from the rates computed by Coe and Fitch and by Smith. In addition, μ_j values over the range 10–30 mm in Table 1 are negative, which is highly unrealistic. These are strong indications that one or more of the assumptions behind Equations (3)–(5) have not been met.

An examination of Coe and Fitch's original data reveals that the steep positive slope of $N_s(z)$ between 10 and 30 mm is primarily the result of a large seasonal variation in growth rate synchronized with a sharply defined year class. Evidently, the assumption of a time-invariant function is inadequate to model growth over this range. At sizes larger than 30 mm, the seasonal component of growth is still strong. However, individual year classes have become sufficiently dispersed in the size distribution so that the yearly average growth increment, as presented in Table 1, is representative of the growth experienced by an individual in the yearly average population, $N_s(z)$. As a result, Method 2 should give a more accurate estimate of μ in this example when it is confined to the segment of size distribution above 30 mm.

Table 1. Mortality rates for 5 mm length classes of *Tivela stultorum*, computed from Method 2

(z_j, z_{j+1}) (mm)	μ_j (yr $^{-1}$)
(5, 10)	1.10
(10, 15)	−0.85
(15, 20)	−0.90
(20, 25)	−1.19
(25, 30)	−0.79
(30, 35)	2.91
(35, 40)	0.26
(40, 45)	1.19
(45, 50)	1.04
(50, 55)	0.00
(55, 60)	0.44
(60, 65)	0.78
(65, 70)	1.57
(70, 75)	1.70
(75, 80)	3.40

Table 2. Comparison of mortality estimates for *Tivela stultorum*

Source	Mortality rate (yr $^{-1}$)
Coe and Fitch (1950)	1.1–1.4
Smith (1972)	1.5
Method II – average of μ_j over all sizes	0.7
Method II – average of μ_j over 30–80 mm	1.3
Method I – $\hat{\mu}$ for 30–80 mm	1.1

The fourth entry in Table 2 is the average of the μ_j over the range 30–80 mm, while the last entry is an estimate from Method I over the same range. Both estimates are in good agreement with the rates calculated by Coe and Fitch.

Discussion

The techniques discussed here are most useful when size distributions and growth curves are available, but age distributions can not be easily or accurately determined. Method I provides a simple extension of Baranov's formula to populations in which individual growth rates are changing with body size. It gives a quick estimate of average mortality. Method 2 is a practical procedure if detailed growth data is available. The method provides size-specific mortality estimates when the stationary size distribution is accurately known. Equation (8) does not require explicit determination of the age distribution, nor does it depend on a fitted growth curve, as in Smith's method.

There are few species, if any, which fulfill the required assumptions of stationarity and of time-invariance in growth and mortality rates. Estimates based on these assumptions can be trusted only to the extent that seasonal and year-to-year changes in recruitment and growth are "averaged out" of the data actually used in (3)–(8).

Fishery biologists have often observed that decreasing growth rates result in a relatively narrow size interval being comprised of several year classes among older and larger individuals. In effect, a fairly long temporal record of growth and recruitment fluctuations is compressed into a fairly short segment of the size distribution. As a result, the right hand limb of a size-frequency curve is more convincingly represented by average (with respect to time) values for growth and an assumption of an average, constant recruitment.

This argument suggests that Methods 1 and 2 are most applicable to older and larger segments of a population with decreasing individual growth rates. For younger, smaller individuals in seasonally breeding populations, the first few year classes can usually be distinctly seen in the size distribution, and techniques based on age distributions can be employed. Thus, a hybrid approach may provide the most accurate mortality estimates for many species.

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Received October 1, 1976